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Annual Nutrient Cycles in a Marine Microcosm

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16. ABSTRACT

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Annual Nutrient Cycles in a Marine Microcosm

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ABSTRACT

Concentrations of ammonia, nitrate plus nitrite, phosphate, and silicate measured in microcosms at weekly intervals during one full year of operation are compared with concurrent data from adjacent Narragansett Bay and with data from a year-long survey of the bay taken in 1972—1973. The major features of the annual cycles for each nutrient in the bay were reflected in observations from nine microcosm tanks. This indicates that the forces driving the cycles in the bay must have counterparts in the microcosms and that the general features of chemical cycling were similar. Some of the small differences in timing between the behavior in the microcosms and the bay provide insight into the causal factors operating in both bay and tanks. This is the first demonstration that such living models of a coastal marine ecosystem will maintain themselves in reasonably normal condition through a complete annual cycle. It appears that the presence of sediment and associated organisms have a crucial influence on the annual cycles of nutrients and probably other substances. Experimentation with the microcosms should help elucidate the processes operative in such systems.

In nature the concentrations and fluxes of nutrients are important features influencing the lives of organisms and may often control the abundance and kinds of species present. It is also true, however, that the biology of the ecosystem influences the concentrations and fluxes of nutrients and that much can be learned about the activities of organisms in an ecosystem by examining nutrient concentrations

and the ways they change with time and biological activity. It seems likely that in all shallow coastal regions a considerable fraction of the nutrient recycling is carried out on and in the sediments, the proportion varying in some inverse way with the depth of water.

Narragansett Bay, Rhode Island, is a weakly stratified estuary with an average depth of 9 m. Concentrations of nutrients in the water undergo marked seasonal variation, with a minimum in the early spring and a peak in the late fall (Smayda, 1957; Kremer and Nixon, 1978). Although a quantitative explanation of the annual variation in nutrient concentrations is not yet available, interaction with the sediments clearly plays a very important role (Nixon, Oviatt, and Hale, 1975). Narragansett Bay is a coupled pelagic—benthic system, with most of the primary production occurring in the plankton but with a strong benthic contribution to the overall chemical cycling.

A set of 12 marine microcosms was established in 1976 at the Marine Ecosystems Research Laboratory (MERL) of the University of Rhode Island. Each microcosm is a cylindrical tank standing 5.5 m high and holding 13.4 tons of water (Pilson et al., 1977, 1979). The intention was to establish coupled pelagic—benthic systems analogous to Narragansett Bay. The bay serves as a source of water and sediment and as a reference ecosystem. In designing the microcosms at MERL, we had little prior experience to draw on. We hoped to run the systems continuously for as long as a year, and no one knew whether it would be possible to maintain reasonably normal conditions in containers for such a long time. We did not know if adjustments of the nutrient concentrations would be required or what the effect of having sediment in the tanks would be on a long-term basis.

During the first year of operation of the MERL microcosms, we made no attempt to change the nutrient concentrations (with one minor exception). We wished to discover how well the microcosms replicated each other with regard to nutrient concentrations and how their behavior compared with that of adjacent Narragansett Bay. In this paper the inorganic nutrient concentrations measured at weekly intervals through an annual cycle are compared in replicate within treatments in the microcosms, between treatments in the microcosms, with concurrent data at one station in the lower west passage of Narragansett Bay, and with data gathered in a 1972—1973 survey of Narragansett Bay. The changes of nutrient concentrations in the microcosms are also compared with nutrient fluxes from the benthos.

METHODS

Description of the Microcosms

Nine microcosm tanks—the number was later increased to 12 (Fig. 1)—were set up outdoors adjacent to lower Narragansett Bay (Fig. 2) alongside a platform providing access to each tank (Pilson et al., 1979). The tanks were provided with the capacity for heating and cooling, but this was not used (except to prevent ice formation in January) so that the temperature followed an annual cycle similar to that in Narragansett Bay (Fig. 3).

In the normal mode of operation, water from Narragansett Bay at the Graduate School of Oceanography (GSO) dock was pumped (with a diaphragm pump shown to be nondestructive to zooplankton) from a depth of about 2 m below the surface to a header

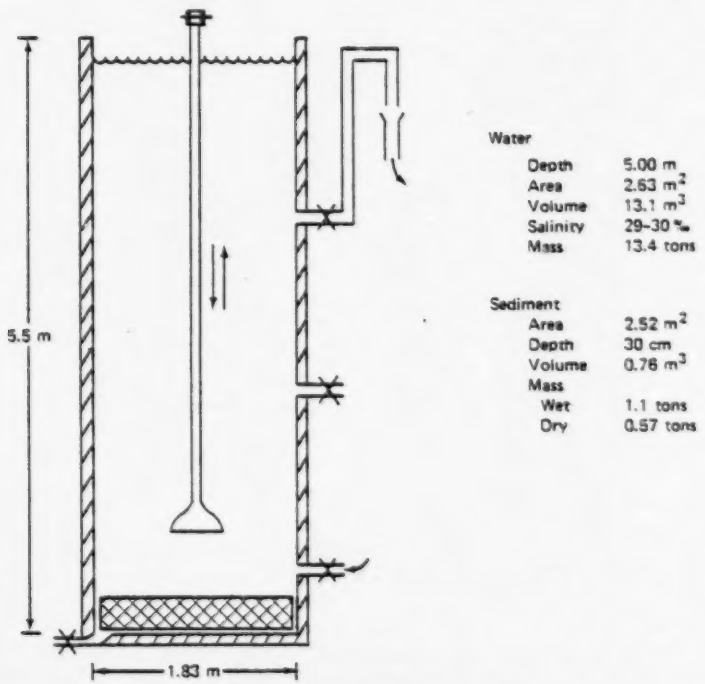

Fig. 1 Cross section of one of the 12 MERL microcosm tanks showing the mixer, sediment container, route of water flow through the tank, and certain physical characteristics.

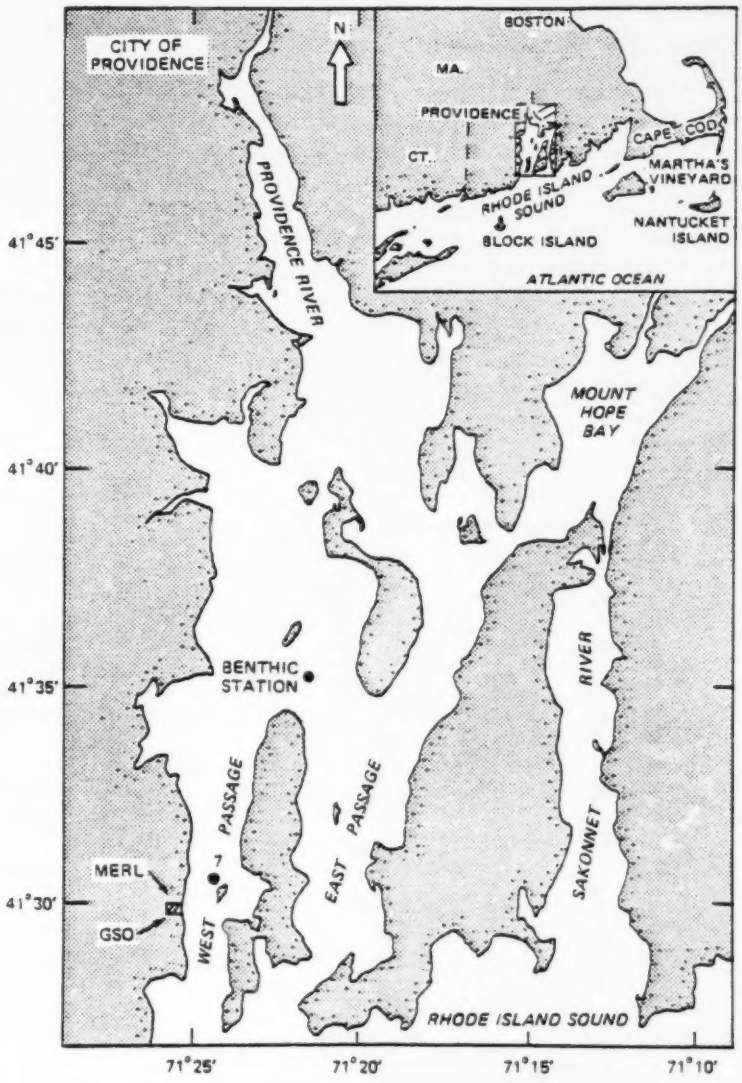

Fig. 2 Map showing locations of the microcosm laboratory at the Graduate School of Oceanography (GSO), University of Rhode Island, on the shore of Narragansett Bay, and the benthic station from which sediments were taken for use in the microcosm tanks. The numbered location (7) refers to one of several stations occupied once each 2 weeks during a year-long survey in 1972–1973. Data from the survey have been used for certain comparisons with the MERL results.

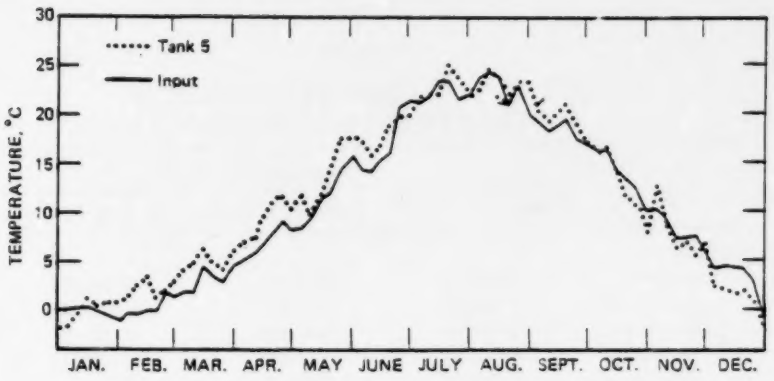

Fig. 3 Temperature of MERL Tank 5 measured by continuously recording thermocouple during the period from August 1976 to September 1977. Input temperatures were measured in the header tank, a part of the water supply system which, because it is continuously running, follows the bay temperature to within less than 2 °C.

tank and allowed to flow by gravity through a series of flow-control devices into each tank at a rate sufficient to replace the water in each tank in 27 days. This was done to allow a continuous introduction of pelagic species and larvae of benthic organisms to the tanks.

Any surface exposed to seawater rapidly becomes fouled, and the developing community on the walls could quickly dominate the total production and respiration in containers such as the MERL microcosms. Since we wished to maintain a primarily planktonic productivity, the walls of the tanks were cleaned regularly. A stainless-steel ring, just smaller than the diameter of the tanks and bearing nylon brush bristles around its perimeter, was lowered and raised in each tank. This removed most of the fouling organisms. This cleaning was supplemented as necessary by hand brushing the accessible region near the top of each tank. The cleaning process was repeated at intervals of about twice weekly in the summer and once each several weeks in the winter. Some resistant organisms could not be removed by these techniques, but overall the fouling community was prevented from developing an appreciable biomass.

Sediment and associated organisms were collected in August 1976 from a region north of Conanicut Island (Fig. 2), loaded into fiberglass containers, and placed in the bottom of the microcosm tanks. The tanks were then filled with bay water (an operation which took about 24 hr), and the steady slow flow started. From August

TABLE 1

OUTLINE OF MERL EXPERIMENTAL TREATMENTS, 1976—1977

Year	Treatment		
	Tanks 1, 5, and 8	Tanks 3, 4, and 6	Tanks 2, 7, and 9
1976			
August	Control	Control	Control
September	Control	Control	Control
October	Control	Control	Control
November	Control	Control	Control
December	Control	Control	Oil
1977			
January	Batch	Batch	Batch
February	Control	Batch	Oil
March	Control	Batch	Oil
April	Control	Batch	Oil
May	Control	Batch	Oil
June	Control	Batch	Oil
July	Control	Batch	Oil
August	Control	Recovery	Recovery
September	Control	Recovery	Recovery

through November all nine tanks were run identically (Table 1). In December, we began to use three of the tanks for oil experiments, which involved adding low concentrations (about 180 ppb) of No. 2 fuel oil. These experiments will be discussed elsewhere (Gearing et al., 1979; Elmgren et al., this volume).

In late December 1976 the pipes froze, and all tanks were without input water during January 1977. To assess the effects of operating the tanks without the slow-flow input water, we maintained three tanks with no input water (i.e., in "batch mode") until Aug. 1, 1977.

Nutrient Concentrations

The tanks were mixed by a mechanical plunger for 2 out of every 6 hr, and dye studies showed that, with the mixers operating, the tanks were uniformly mixed in 10 min (Nixon et al., this volume). Therefore, samples for nutrient analyses were nearly always taken after at least 30 min of mixing and while the mixers were still running. Samples were drawn by siphon from the mid-depth position in the tanks, or from depths of 0.1, 2.5, and 4.5 m, and combined. Nutrient samples were drawn weekly during the first year of

operation from each of the nine tanks. Samples were also taken by Niskin bottle sampler, from a depth of approximately 2 m, at the GSO dock near the location of the lines feeding the input pumps to the tanks. The samples were filtered through Millipore filters by using a 50-ml plastic syringe equipped with a stainless-steel filter holder. Filtered samples were discharged into plastic bottles that had been cleaned and soaked in deionized water. Analysis was usually performed on the same day; if not, the samples were frozen until analysis. Concentrations of nitrate plus nitrite, ammonia, silicate, and phosphate were determined by procedures recommended by Frederick and Whitledge (1972), on a four-channel Technicon Autoanalyzer II.

Benthic Flux Measurements

Box cores (10 by 30 cm) were taken from each tank at approximately monthly intervals and the net flux of nutrients from the sediments in these cores was measured as follows.

A Plexiglas box core (Fig. 4) was lowered into the microcosms, guided by a three-arm positioner on the tank surface, so that the location of the core could be mapped. The corer was set about 10 cm into the sediment, the depth being regulated by legs on the corer. A pole within the metal rod was used to close the corer by sliding two pieces of metal across the bottom of the core to meet in the center. The corer and core were then lifted to the water surface; the depth-regulating legs were removed; and a tight-fitting seawater-filled Plexiglas caddy was slipped under the core to prevent leakage. Caddy and corer were then lifted from the water and removed to a water bath for incubation at ambient bay temperature. Controls without sediment were incubated at the same time.

A centrifugal pump and hoses were flushed with HCl and hot fresh water before each run. All air was expelled from the primed pumping system and the core. Fresh seawater from the water bath was flushed over the open core for 15 min. During this period, initial samples were taken from the exit opening on the core top. Then the hoses were removed, and the corer was plugged. After the run, final samples for oxygen, nutrients, and suspended particulates were drawn from over the core, and oxygen and nutrient samples were drawn from water incubated in control containers. Duration of the runs depended on oxygen saturation levels and rates of metabolism, varying from 3 to about 20 hours, mostly because of variations in ambient temperature.

Oxygen samples were withdrawn by syringe, transferred to 60-ml BOD bottles, and fixed for titration in the laboratory (Strickland and Parsons, 1968). Samples for nutrients were filtered through Gelman

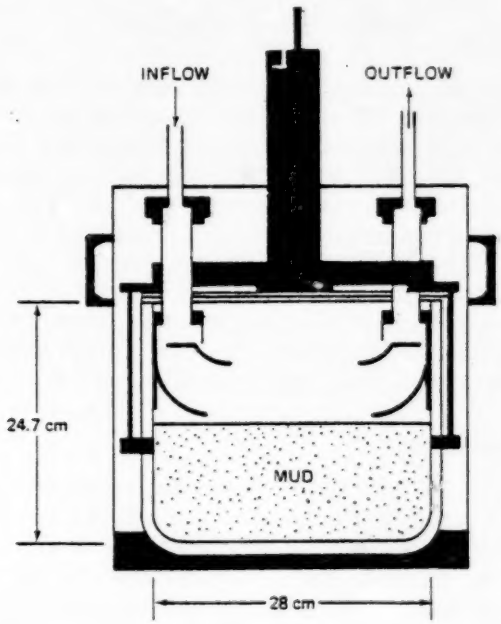

Fig. 4 Diagram of the box core used to collect samples of sediment for incubations to measure benthic fluxes.

Type A glass-fiber filters and preserved (Degobbis, 1973; Gilmartin, 1967) for laboratory analysis of ammonia (Solorzano, 1969), nitrate—nitrite (by Technicon Autoanalyzer), and inorganic and dissolved organic phosphate (Strickland and Parsons, 1968). Oxygen and ammonia determinations were made the same day the samples were taken, whereas samples for other analyses were frozen in polyethylene bottles.

RESULTS

Phosphate

Phosphate concentrations in individual tanks varied somewhat in detail from week to week and in the timing of certain events, but the overall pattern during the course of the year in all tanks showed the same major features [Fig. 5(a)]. Tank-to-tank variability in the other treatment groups was similar to that in the control tanks. The groups of tanks also behaved similarly [Fig. 5(b)] during the period from

Aug. 16 to Dec. 31, 1976, when tanks 1, 5, and 8 and 3, 4, and 6 were treated identically. From Jan. 1 to Feb. 15 all tanks were deprived of input water, and tanks 3, 4, and 6 remained in batch-type operation until July 31, 1977. The batch tanks, isolated from the bay input water, showed the same trend as the control tanks, which were flushed from Feb. 15 on. The summer increase of phosphorus must be driven primarily by events within the tanks and not by the input water [Fig. 5(b)]. The increase in average phosphate concentration in the three batch tanks in February 1977 was caused by the addition of phosphate equivalent to 2 μg atoms/liter to tank 4 on Feb. 14. Within a short period of time, the

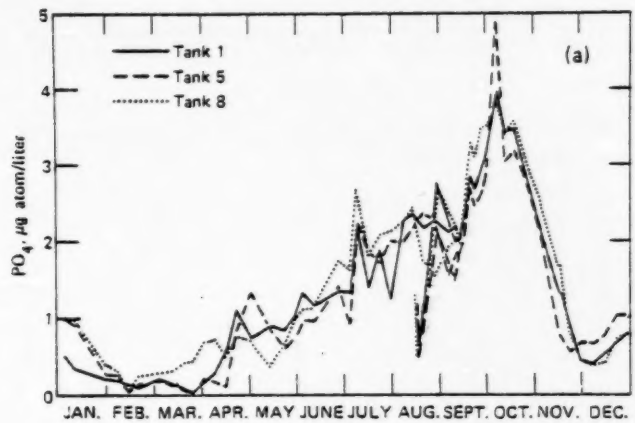

Fig. 5 Concentrations of dissolved reactive phosphate in MERL tanks and in Narragansett Bay. In MERL tanks measurements were made once per week from Aug. 16, 1976, to Sept. 12, 1977. In Narragansett Bay measurements were made once per week during the same period in 1976—1977 and approximately once each 2 weeks in 1972—1973. (a) Individual control tanks 1, 5, and 8. (b) Mean values from control tanks 1, 5, and 8 and experimental tanks 3, 4, and 6. All tanks were treated identically and were in flow-through operation until Dec. 30, 1976, when flow through ceased. Then all tanks were in batch operation until Feb. 16, 1977. After that, control tanks were back in flow-through operation, but experimental tanks were maintained with no input water until July 21, 1977. (c) Mean values from control tanks 1, 5, and 8 and individual values from Narragansett Bay at the GSO dock (near the intake to the pumps) in 1976—1977. Concentrations at bay station 7 in 1972—1973 (from Nixon, Kremer, and Oviatt, unpublished data).

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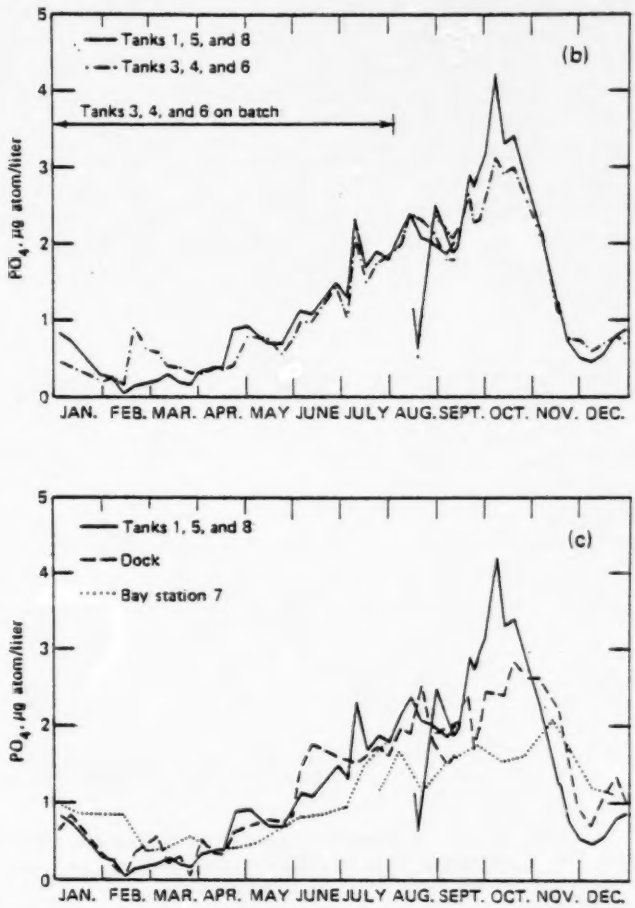

Fig. 5 (Continued)

concentration in tank 4 returned to values similar to those in the other tanks.

When first measured about 2 weeks after filling, phosphate concentrations in all tanks were somewhat lower than those in the bay, but they rose to and slightly exceeded bay values until the major decline in November [Fig. 5(c)]. This decline began earlier in the tanks than in the bay, indicating that it was caused by conditions within the tanks and could not have been caused by washout of phosphate. After the decline the concentrations reached a minimum in February and then began a steady upward trend in both the bay

and the tanks, coming close in September to the concentrations of the previous year.

Thirteen stations in Narragansett Bay (Fig. 2) were sampled every 2 weeks from July 26, 1972, until Aug. 1, 1973. Comparing data from station 7, nearest the GSO dock, with those from the dock in 1976—1977 provides some indication of year-to-year variation of phosphate concentrations in Narragansett Bay [Fig. 5(c)]. The same annual trend is evident for both bay data sets, but the concentrations during the late summer and fall of 1976 and the late summer of 1977 were higher than they had been 4 years before. The phosphate concentrations in Narragansett Bay differed more from year to year than from bay to microcosm tanks in the same year.

Inorganic Nitrogen

Ammonia concentrations, measured weekly in three tanks, were plotted [Fig. 6(a)] to show the correspondence between tanks. In subsequent plots the ammonia and nitrate-plus-nitrite concentrations

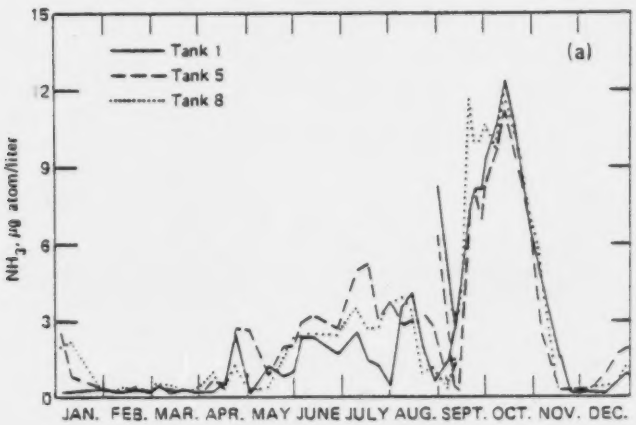

Fig. 6 Concentrations of nitrogen nutrients in MERL tanks in 1976—1977 and in Narragansett Bay in 1976—1977 and 1972—1973. Measurement frequency and other details are given in the legend for Fig. 5. (a) Ammonia in individual control tanks 1, 5, and 8. (b) Total inorganic nitrogen (ammonia and nitrate plus nitrite) in control and experimental (batch) tanks. (c) Total inorganic nitrogen in control tanks and in Narragansett Bay at the GSO dock for 1976—1977 and at bay station 7 in 1972—1973.

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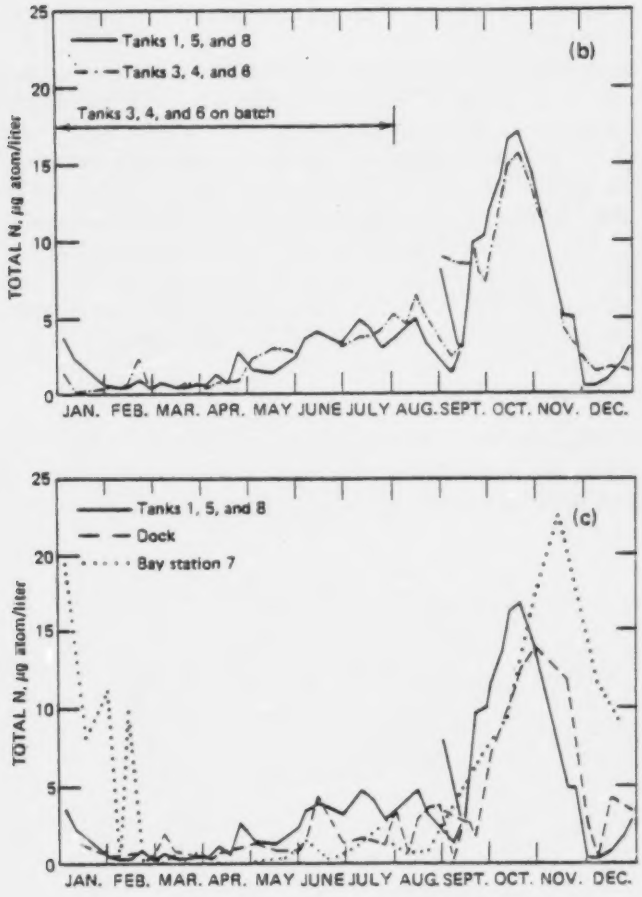

Fig. 6 (Continued)

are summed to give the concentration of total dissolved inorganic nitrogen.

Nitrogen concentrations differed little between control and batch tanks [Fig. 6(b)]; this indicated that isolation from bay input water had a negligible effect on the concentration of inorganic nitrogen. Again, the same major features of the annual cycle were observed in the tanks and in the bay [Fig. 6(c)]. As was the case for phosphate, the drop in the concentrations of the nitrogen nutrients in the microcosm tanks in November happened earlier than did that in the

bay; thus it could not have been driven by events in the bay or by washout with low nutrient water from the bay.

Comparing the dock data in 1976—1977 with those from station 7 in 1972—1973 [Fig. 6(c)] again indicated greater differences between years in the bay than between bay and tanks during the same year.

Silicate

Silicate concentrations in tanks 1, 5, and 8 followed each other quite closely during the year [Fig. 7(a)]. An indication of the differences between the groups of three tanks each is given by the plots for the period from Aug. 16, 1976, through Feb. 15, 1977, for tanks 1, 5, and 8 and 3, 4, and 6 [Fig. 7(b)] when these tanks were all treated identically. The concentrations of silicate also did not differ between tanks in batch-mode operation and those in the flow-through mode [Fig. 7(b)]. Silicate concentrations in the tanks also corresponded to those observed at the GSO dock [Fig. 7(c)]. Year-to-year variation in Narragansett Bay was considerable, with the concentrations in January and February being higher in 1973 than in

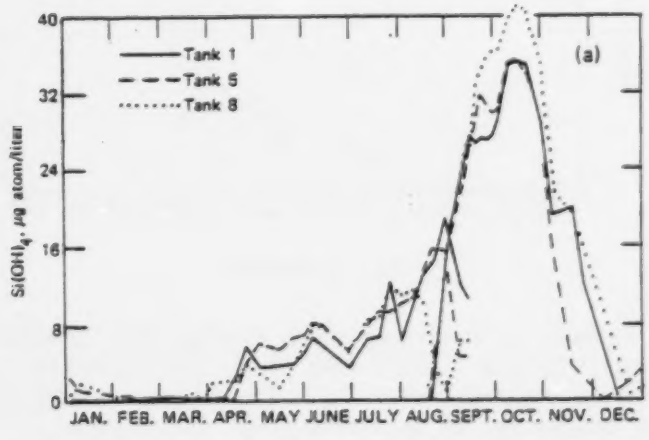

Fig. 7 Concentrations of dissolved silicate in MERL tanks in 1976—1977 and in Narragansett Bay in 1976—1977 and in 1972—1973. Other details are given in the legend for Fig. 5. (a) Silicate in individual control tanks 1, 5, and 8. (b) Mean values from control tanks 1, 5, and 8 and experimental tanks 3, 4, and 6. (c) Mean silicate concentrations in control tanks and in Narragansett Bay at the GSO dock in 1976—1977 and at bay station 7 in 1972—1973.

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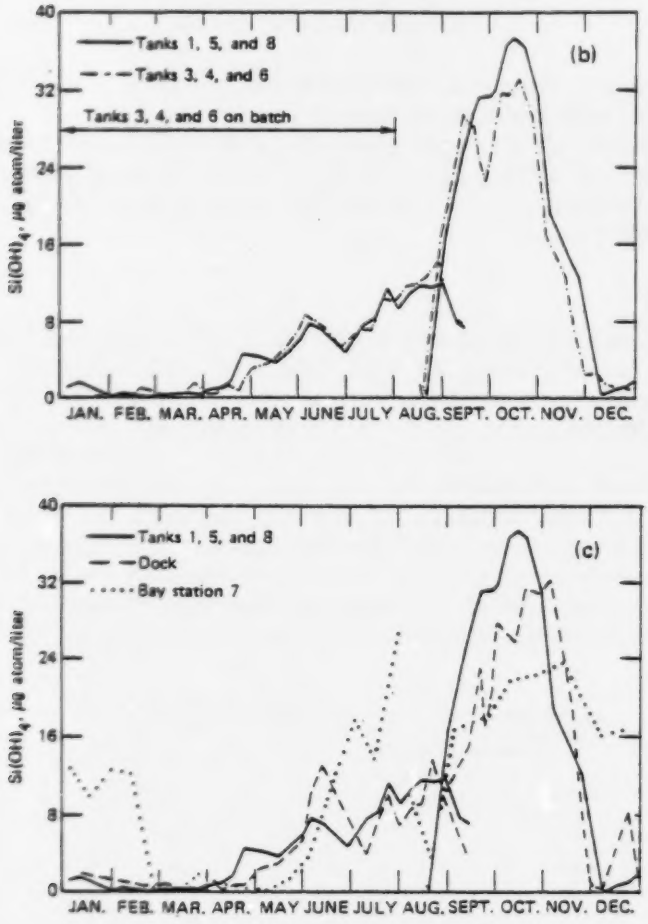

Fig. 7 (Continued)

1977, whereas the concentrations in October and November were higher in 1976 than in 1972 [Fig. 7(c)]. The differences between years in the bay were greater than those between tanks or those between the bay and the microcosm tanks within 1 year.

Benthic Fluxes of Oxygen and Nutrients

Flux data showed considerable variability. Since no differences could be detected ($P < 0.05$) among treatments, values for all nine tanks were averaged each month (Table 2). The high variance in the

TABLE 2

MEAN VALUES FROM NINE TANKS EACH TIME FOR THE FLUXES OF DISSOLVED SUBSTANCES INTO (−) AND OUT OF (+) SEDIMENTS FROM THE MERL TANKS*

Date	Oxygen	Nitrogen				Total phosphorus	Silicate
		NH_3	NO_3	NO_2	Total		
1976							
Aug. 23–27	−2750 ± 1500	131 ± 70			131		
Sept. 21–24	−1750 ± 750	140 ± 58	−5 ± 20	1 ± 5	136	0 ± 17	143 ± 88
Oct. 18–22	−1250 ± 813	59 ± 43	−2 ± 26	2 ± 2	59	3 ± 6	76 ± 72
Nov. 15–19	−813 ± 563	18 ± 4	−6 ± 15	0 ± 1	12	0 ± 3	8 ± 19
1977							
Jan. 11	−875 ± 375	8 ± 5	−0.4 ± 4	−0.1 ± 0.4	7	4 ± 5	22 ± 9
Mar. 21–27	−438 ± 563	8 ± 13	2 ± 3	0.1 ± 0.4	10	4 ± 3	−7 ± 15
Apr. 17–22	−1188 ± 375	41 ± 21	4 ± 3	1 ± 1	46	3 ± 3	26 ± 29
May 15–19	−1250 ± 625	44 ± 29	3 ± 5	1 ± 1	48	11 ± 10	54 ± 60
June 13–16	−2000 ± 1000	56 ± 33	1 ± 6	2 ± 1	59	8 ± 9	18 ± 52
July 11–14	−2438 ± 938	98 ± 49	7 ± 9	3 ± 2	108	12 ± 9	115 ± 112
Aug. 1–4	−1688 ± 375	68 ± 31	12 ± 31	1 ± 2	81	7 ± 7	80 ± 94
Aug. 29–Sept. 1	−2063 ± 563	109 ± 34	4 ± 49	2 ± 3	115	3 ± 6	101 ± 75
Sept. 20–23	−1313 ± 375	80 ± 23	1 ± 7	−0.3 ± 2	81	18 ± 14	

*Values are microgram atoms of the element fluxing through 1 m^2/hr ± one standard deviation.

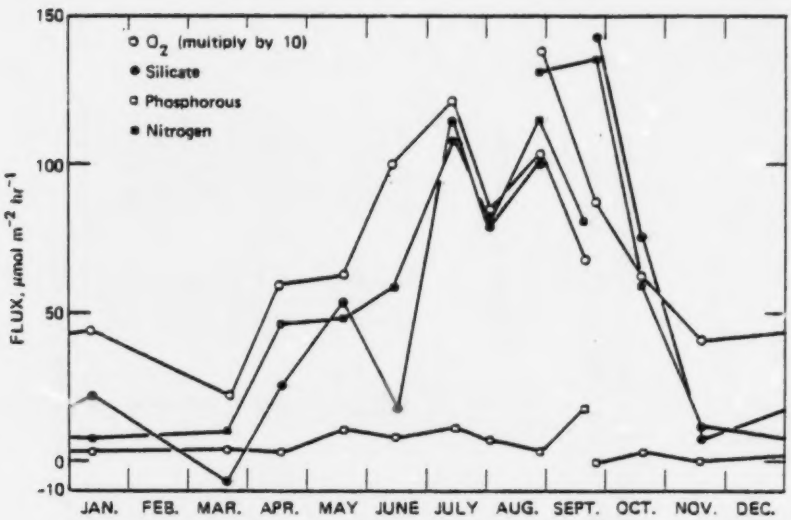

Fig. 8 Mean values for the uptake of oxygen and the flux of nitrogen (ammonia plus nitrate plus nitrite), silicate, and total dissolved phosphorus across the sediment–water interface in box cores taken from each of the nine MERL microcosms each month and incubated at the temperature of the tanks.

data was discouraging and must account for some of the scatter observed in the mean values (Fig. 8). Nevertheless, a distinct seasonal pattern was evident for all substances measured, with the rates being highest in the summer and decreasing to low winter rates by November. Low rates were maintained until approximately April, when marked increases occurred.

Flux data have also been obtained from Narragansett Bay using domes incubated in situ (Nixon, Oviatt, and Hale, 1975; Nixon et al., 1980). These data and the MERL data were plotted (as in Fig. 8), and estimated values for the whole year were obtained by integrating under the curves (Table 3).

DISCUSSION

Agreement Between Microcosms and Bay

From the data presented here, it seems clear for the first time that large-scale temperate marine microcosms that are self-maintaining over an annual cycle can be developed. One of the most

TABLE 3

INTEGRATED VALUES FOR ANNUAL FLUX OF SUBSTANCES ACROSS THE SEDIMENT–WATER INTERFACE, AVERAGED FROM THREE STATIONS IN NARRAGANSETT BAY* AND FOR THE MERL TANKS†

	Field, mol m^{-2} $year^{-1}$	Microcosms, mol m^{-2} $year^{-1}$	% of field
Oxygen (as O_2)	11.6	5.13	44
Carbon	11.6	5.13	44
Ammonia	0.87	0.34	41
Nitrate plus nitrite		0.073	
Dissolved total phosphorus	0.121	0.062	51
Silicate	2.24	0.44	20

*One station was in the region just north of Conanicut Island where MERL sediments were obtained.

†For oxygen the flux was always downwards, but for all other substances the mean flux was upwards. The carbon flux was not measured but was taken as 1.0 times the flux of O_2.

remarkable features of the MERL microcosms is the striking similarity in the timing and magnitude of seasonal patterns of dissolved nitrogen, phosphate, and silicate in the tanks and in Narragansett Bay. Although such agreement is encouraging and rewarding, it is also puzzling. We generally assume that, after more than 40 years of study, the basic processes underlying the nutrient dynamics of coastal marine waters are well understood. Much of what we assume to be true of nutrient cycling suggests that the magnitude and perhaps the timing of the seasonal nutrient cycles in the tanks should be different from those observed in the bay.

Input of nutrients from rivers and sewage, release from the sediments, biological uptake, return to sediments in particulate form, and washout from the bay are all important. Presumably, the relative magnitudes of these processes must vary from year to year, causing the observed year-to-year variation in average concentrations in the bay. The MERL microcosms were not subject to all these processes, however, and initial thoughts were that they could not, therefore, closely follow the bay.

It was predicted that sediment–water exchange processes would be important in the overall dynamics of the system. However, the ratio of water volume to sediment surface area in the microcosms is about half that of Narragansett Bay as a whole and 70% that of the middle of West Passage, where the sediments originated. If the flux

of nutrients from the bottom were determined by a long history of acclimation to input from the overlying water, the fluxes from the sediments in the tanks might be expected to have remained similar to those in the field, and the result might have been higher concentrations in the microcosms. In fact, the average fluxes of various nutrients in the tanks ranged from 20 to 55% of those observed in the field, but water-column concentrations maintained in the tanks were not clearly distinguishable from those in the field. If the benthic fluxes were indeed as low as the measurements indicate, water-column concentrations similar to those in the bay could be achieved if there were a correspondingly lower return transport of particulate organic matter from the water column to the bottom.

The annual total planktonic productivity in the MERL tanks during 1976—1977 was about 100 g C/m^2 (Vargo, unpublished data), and current estimates indicate that production on the walls may have been about 15 to 20 g C/m^2 (expressed per unit area of tank water surface). Phytoplankton production in Narragansett Bay as a whole has not been estimated from direct measurement. Nixon, Oviatt, and Hale (1975) estimated annual benthic respiration alone to be 140 g C/m^2, based on a conversion from measured oxygen uptake. A simulation model (Kremer and Nixon, 1978) provided estimates of primary production of 99 g C m^{-2} year^{-1} for the whole bay, with a range of 60 to 155 g C m^{-2} year^{-1} in eight regions, and 97 g C m^{-2} year^{-1} for the middle of the West Passage. Direct measurements of pooled samples from one station in the West Passage incubated in a light gradient box gave an estimate of 308 g C m^{-2} year^{-1} (Furnas, Hitchcock, and Smayda, 1976). The evidence is equivocal, but it is not impossible that production in the tanks was half that in the field. A lower production could lead to a lower transport of particulate organic matter to the sediment and a lower rate of return flux to the water. The higher rate of vertical water mixing developed in the MERL tanks, in comparison with the bay (Nixon et al., this volume), might keep particles in suspension longer than in the bay, but it is not clear what effect this would have.

Summer Increase in Nutrient Concentrations

The summer increase in control-tank nutrient concentrations could not be explained by assuming that tank concentrations passively followed those in the bay according to the flushing of the tanks by bay water. The half-life of water in the tanks was 19 days; thus tank concentrations would have lagged behind those in the bay. In fact, concentration changes in the tanks often occurred slightly earlier. Although the batch tanks were isolated from the bay, they

TABLE 4

MEAN INCREASE IN NUTRIENT CONCENTRATIONS IN TANKS 1, 5, AND 8 DURING THE 105-DAY PERIOD FROM MAR. 28, 1977, TO JULY 11, 1977, COMPARED WITH THE MEASURED FLUXES FROM THE SEDIMENTS DURING THIS TIME

	PO_4	Total N	$Si(OH)_4$
Concentration increase, μg atom/liter	2.35	4.16	7.35
Mean flux, μg atom m^{-2} hr^{-1}	8.5	65	53
Ratio: $\frac{\text{observed flux}}{\text{required flux}}$	2.0	7.9	3.6

nevertheless followed almost exactly the same pattern as the control tanks. With only the sediments as a source, nutrient concentrations in the tanks followed those of the bay very closely, even though the bay is supplied by other sources as well.

The observed increase of nutrient concentrations in the MERL tanks can be quantitatively accounted for by the flux from the sediments (Table 4). The nutrient fluxes from the sediments were greater than required to provide the increased concentrations in the water; the excess was presumably consumed in biological production and returned in particulate form to the sediments.

Taft and Taylor (1976) ascribed a summer phosphate maximum observed in other east coast estuaries to anoxia in the bottom water and sediments (and consequent release of PO_4 from insoluble ferric phosphate). This explanation seems unlikely to hold for the nitrogen nutrients, however, and possibly not for silicate. Since the tanks were well mixed and oxygen concentrations in the water remained high (unpublished data), this explanation does not hold for phosphate in the tanks either.

Fall Decline in Nutrient Concentrations

The observed decrease in nutrient concentrations during the late fall in Narragansett Bay was ascribed by Nixon, Oviatt, and Hale (1975) (who made the calculation for the nitrogen nutrients only) to washout into adjacent Rhode Island Sound. In the tanks the striking decrease in all nutrient concentrations during the late fall cannot be accounted for by washout. Since the decrease in the tanks preceded that in the bay by about 2 weeks, the input of high-nutrient water

from the bay and the output of low-nutrient water from the tanks would have tended to prevent the decline of nutrient concentrations in the tanks at this time. The nutrients left the water column in the tanks by a route not yet evident.

It is also difficult to explain the fall nutrient decrease by invoking biological uptake. The concentration of phytoplankton was at a minimum during the early part of the decrease (Fig. 9 and Table 5), and an algal bloom began about halfway through the decrease, which was not exactly coincident for the different nutrients. For purposes of calculation, we have taken the earlier part of the nutrient decrease, before the onset of the bloom, where the difficulty is greatest. Two sets of calculations are presented (Table 6). In the table the change in chlorophyll a during the first month of nutrient decline is shown, together with the probable change in nutrient concentrations calculated on the basis of an assumed set of ratios obtained from Strickland (1965) for a "coastal crop" of plankton, mainly diatoms, growing with excess nitrogen and phosphorus. The C/Si value of 10 was used, this being intermediate between the extremes discussed and that chosen by Kremer and Nixon (1978) and measured by Furnas, Hitchcock, and Smayda (1976). The observed decreases in nutrient concentrations were all much greater than could be accounted for by the very small increase in the phytoplankton standing stock. Examination of Vargo's data (1976) suggests that similar anomalies can occur in Narragansett Bay.

In the third column of Table 6, the total planktonic production of carbon is shown. If we assume that all the production was lost from the water columns in particulate form (except for the ~3% appearing as an increase of cell biomass) and that no regeneration of nutrients took place during this time, it is possible to account for the decrease in nitrogen but not for the decrease in phosphate or silicate. If nutrient mass-balance calculations are based on ratios derived from Redfield, Ketchum, and Richards (1963), the discrepancy is greater.

It remains to be considered whether uptake on the walls of the tanks could reduce the nutrient concentrations in the water column. The brushing does not completely remove organisms from the walls. We do not have measurements of production and respiration on the walls for the period in question. During 1978, however, a number of measurements were made by estimating total system metabolism from diurnal oxygen changes and comparing the estimates of primary production with measurements made in bottles in the water column only (Oviatt et al., unpublished data). Measurements were made in two tanks on three occasions each, with the following results:

Mean production on walls = 18% of total
Mean respiration on walls = 13% of total

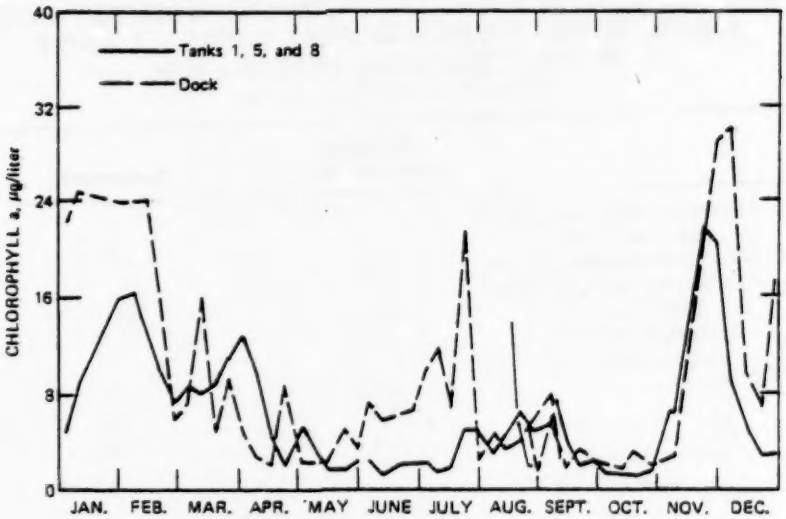

Fig. 9 Mean concentrations of chlorophyll a in MERL control tanks 1, 5, and 8 and in Narragansett Bay at the GSO dock from Aug. 16, 1976, to Sept. 12, 1977.

TABLE 5

MEAN CONCENTRATIONS OF DISSOLVED INORGANIC NUTRIENTS, CHLOROPHYLL a, AND PRIMARY PRODUCTION DURING THE FALL DECREASE IN MERL TANKS 1, 5, AND 8

Date	Total N, µg atom/liter	PO_4, µg atom/liter	$Si(OH)_4$, µg atom/liter	Chlorophyll a, µg/liter	Production, mg C m^{-2} day^{-1}
Oct. 7	13.7	4.23	36.6	1.41	86
Oct. 12	16.4	3.31	25.0	1.21	68
Oct. 18	17.0	3.42	24.5	1.14	
Oct. 22					81
Oct. 27	14.2	2.81	31.2	1.59	
Nov. 4	10.3	2.19	18.9	1.95	

TABLE 6

COMPARISON OF NUTRIENT CHANGES OBSERVED AND CALCULATED FROM CHANGE IN CHLOROPHYLL a AND OBSERVED PRODUCTION IN MERL TANKS 1, 5, AND 8 DURING THE 28-DAY PERIOD FROM OCT. 7 TO NOV. 4, 1976*

	Change in chlorophyll a		Production
Observed mean value for C, mg C m^{-2} day^{-1}			78
Observed increase, μg/liter	0.54		
Calculated value, μg atom C m^{-2} hr^{-1}	8.4		271
Calculated decrease, μg atom m^{-2} hr^{-1}			
P	0.19		6
N	2.87		93
Si	0.3		10
Observed decrease, μg atom m^{-2} hr^{-1}			
P		15.2	
N		25.3	
Si		132	

*Calculations are based on weight ratios from Strickland (1965) (C/chlorophyll a = 25, N/chlorophyll a = 10, and P/chlorophyll a = 1.5) and Kremer and Nixon (1978) (C/Si = 10).

If these values apply to the fall period in 1976 (and we have no reason to think they would not), then including the metabolic activities on the walls would not appreciably change the conclusions and would not be sufficient to eliminate the anomalies apparent in the nutrient decreases.

It seems unlikely that direct uptake by sediments could account for the decrease in nutrient concentrations, since virtually all measurements at this time showed a net flux of nutrients upwards into the overlying water (Fig. 8). Possibly there was uptake by particles of suspended sediment as the temperature cooled, but it is not clear why this would have occurred when the whole bottom sediment was not absorbing nutrients.

Nutrients seem to be returned to the sediments during the period of fall cooling, but (except for nitrogen, for which a plausible case might be made) the mechanism at present eludes us.

Since the fall decline in nutrient concentrations in the tanks more or less paralleled that in the bay but the explanations advanced for the bay appear not to hold in the tanks, it is possible that they do not hold in the bay either.

The Annual Concentration Cycle

The variation in nutrient concentrations observed through the course of the year in the bay (see Smayda, 1957; Pratt, 1965; Kremer and Nixon, 1978) is not fully understood. In Narragansett Bay the phosphate cycle appears to be typical of east coast estuaries for which similar data exist (Taft and Taylor, 1976), but the peaks in both 1972 and 1976 occurred 1 or 2 months later than they have in Pamlico River, N. C., and in Chesapeake Bay.

Clearly, the recycling mechanisms operative in the tanks were adequate to maintain the annual cycles within the range observed in Narragansett Bay. Individual mechanisms and rates are much faster than implied in the annual changes, however. Gross flux rates from the sediments, for example, are greater than needed to account for water-column changes. Even the measured flux rates must be the result of numerous uptake, release, and exchange processes operating on short-to-long time scales. It is remarkable that the integrated resultant cycles are so "natural."

No explanation seems satisfactory to account for the fact that nutrient concentrations in the microcosms follow those in the bay more closely than the bay itself replicated from year to year. Perhaps further experiments with the microcosms will lead to a better quantitative understanding of the functioning of Narragansett Bay and similar coastal marine ecosystems. In any case, it seems that these complex microcosms adjust themselves to operate in ways that follow the major trends in the adjacent bay, even when they are to a considerable extent isolated from the bay. We speculate that this is because of the presence of a thick layer of natural sediment in each tank which acts to buffer the systems and responds to changes in temperature and other seasonal factors in much the same way as does sediment in the bay.

Replication Among Tanks

Individual tanks showed slight variations in the timing of various events, but overall their behavior was similar. The variations in timing, even though relatively small, cause difficulties in the statistical analysis and presentation of data, especially when the concentration changes are large and rapid [Figs. 5(a), 6(a), and 7(a)].

A variation in timing of only 1 or 2 weeks among tanks results in large apparent differences among tanks in any 1 week. It is evident that if only a short-term and limited data set is available, the differences among tanks may by chance seem to be very great when they are caused only by relatively small differences in timing. The conventional plotting of mean data with standard deviations or some other statistical measure of dispersion will often show differences that are either spuriously small or spuriously large. There is no easy way to deal with this, so we provided plots of data from individual tanks to show directly the extent of the variability.

Implications

The record from observations in these microcosms provides several points of interest. Concentrations of all nutrients replicated well between the tanks over the annual cycle. Concentrations were quite similar to those in Narragansett Bay, supporting the view that the biogeochemical behavior of other substances we know less about will also follow their behavior in similar marine coastal waters. By observation in these microcosms, we should be able to learn a great deal about the behavior of natural substances and anthropogenic pollutants in natural systems.

The results have caused us to reexamine to some extent our concepts of nutrient cycling in Narragansett Bay and other coastal regions and will help to refine our quantitative understanding of the various processes operative in shallow bays and estuaries.

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REFERENCES

Degobbis, D., 1973, On the Storage of Seawater Samples for Ammonia Determination, *Limnol. Oceanogr.*, 18: 146-150.

Frederick, G. O., and T. Whitledge, 1972, Autoanalyzer Procedures for Nutrients, in *Chemostat Methodology and Chemical Analyses*, S. D. Parlou (Ed.), pp. 38-60, Special Report 52, Department of Oceanography, University of Washington, Seattle.

Furnas, M. J., G. L. Hitchcock, and T. J. Smayda, 1976, Nutrient—Phytoplankton Relationships in Narragansett Bay During the 1974 Summer Bloom, in *Estuarine Processes*. Vol. 1. *Uses, Stresses, and Adaption to the Estuary*, M. Wiley (Ed.), pp. 118-134, Academic Press, Inc., New York.

Gearing, J. N., et al., 1979, The Rates of Transport and Fates of Petroleum Hydrocarbons in a Controlled Marine Ecosystem, and a Note on Analytical Variability, in *Proceedings of the 1979 Oil Spill Conference*, March 19—22, 1979, Los Angeles, Calif., pp. 555-564, Publication No. 4308, American Petroleum Institute, Washington, D. C.

Gilmartin, M., 1967, Changes in Inorganic Phosphate Concentration Occurring During Sea Water Sample Storage, *Limnol. Oceanogr.*, 12: 325-328.

Kremer, J. N., and S. W. Nixon, 1978, *A Coastal Marine Ecosystem: Simulation and Analysis*, Ecological Studies 24, Springer-Verlag New York, Inc., New York.

Nixon, S. W., J. R. Kelly, B. N. Furnas, C. A. Oviatt, and S. S. Hale, 1980, Phosphorus Regeneration and the Metabolism of Coastal Marine Bottom Communities, in *Marine Benthic Dynamics*, K. Tenore and B. Coull (Eds.), University of South Carolina Press, Columbia, in press.

——, C. A. Oviatt, and S. S. Hale, 1975, Nitrogen Regeneration and the Metabolism of Coastal Marine Bottom Communites, in *The Role of Terrestrial and Aquatic Organisms in Decomposition Processes*, J. M. Anderson and A. MacFadden (Eds.), the 17th Symposium of the British Ecological Society, April 15—18, 1975, pp. 269-283, Blackwell Scientific Publications, Oxford.

Pilson, M. E. Q., C. A. Oviatt, G. A. Vargo, and S. L. Vargo, 1979, Replicability of MERL Microcosms: Initial Observations, in *Advances in Marine Environmental Research*, F. S. Jacoff (Ed.), pp. 359-381, Report EPA-600/9-79-035, Environmental Protection Agency, Narragansett, R. I.

——, G. A. Vargo, P. J. Gearing, and J. N. Gearing, 1977, Investigation of Effects and Fates of Pollutants, in *Proceedings, Second National Conference Interagency Energy/Environment R & D Program*, June 6—7, 1977, Washington, D. C., pp. 513-516, EPA-600/9-77-012, Environmental Protection Agency.

Pratt, D. M., 1965, The Winter—Spring Diatom Flowering in Narragansett Bay, *Limnol. Oceanogr.*, 10: 173-184.

Redfield, A. C., B. H. Ketchum, and F. A. Richards, 1963, The Influence of Organisms on the Composition of Seawater, in *The Sea*. Vol. 2. *Composition of Sea-Water*, M. N. Hill (Ed.), pp. 26-77, John Wiley & Sons, Inc., New York.

Smayda, T. J., 1957, Phytoplankton Studies in Lower Narragansett Bay, *Limnol. Oceanogr.*, 2: 342-359.

Solorzano, L., 1969, Determination of Ammonia in Natural Waters by Phenol Hypochlorite Method, *Limnol. Oceanogr.*, 14: 799-801.

Strickland, J. D. H., 1965, Production of Organic Matter in the Primary Stages of the Marine Food Chain, in *Chemical Oceanography*, J. P. Riley and G. Skirrow (Eds.), pp. 477-610, Vol. 1, Academic Press, Inc., New York.

——, and T. R. Parsons, 1968, *A Practical Handbook of Sea-Water Analysis*, Bulletin 167, Fisheries Research Board of Canada, Ottawa.

Taft, J. L., and W. R. Taylor, 1976, Phosphorus Dynamics in Some Coastal Plain Estuaries, in *Estuarine Processes*. Vol. 1. *Uses, Stresses, and Adaptation to the Estuary*, M. Wiley (Ed.), pp. 79-89, Academic Press, Inc., New York.

Vargo, G. A., 1976, *The Influence of Grazing and Nutrient Excretion by Zooplankton on the Growth and Production of the Marine Diatom,* Skeletonema costatum *(Greville) Cleve, in Narragansett Bay*, Ph.D. Thesis, University of Rhode Island, Kingston.